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On Two Ochotonids (Mammalia, Lagomorpha) from the Later Tertiary of Inner Mongolia[1]

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INTRODUCTION

The fossil record of the mammalian order Lagomorpha in Mongolia and China is a long one, extending back to the late Paleocene with the appearance of *Eurymylus,* the oldest known lagomorph, from the Gashato formation. *Mimolagus,* a lagomorph of unknown age from Kansu, may be allied to *Eurymylus* (Wood, 1957, pp. 417–418). *Shamolagus* and *Gobiolagus* appeared in the late Eocene, and *Gobiolagus, Desmatolagus,* and *Sinolagomys* are known from the Oligocene. After the late Oligocene, although ochotonids were probably present in Asia, there is an absence of lagomorphs from the Asian fossil record until the late Miocene, when the ochotonids discussed herein appeared. Later, in the Pontian and middle Pliocene, *Ochotona* and a possible precursor of *Ochotonoides complicidens* (Bohlin, 1942b, pp. 144–145) represented the family Ochotonidae and *Alilepus* represented the Leporidae. Both families persist in Asia into the Recent.

[1] Publications of the Asiatic Expeditions of the American Museum of Natural History, Contribution No. 153. Recent numbers in this subseries, inadvertently not so designated, are: No. 149, Hooijer, D. A., American Museum Novitates, no. 1346 (1947); No. 150, Hooijer, D. A., American Museum Novitates, no. 1495 (1951); No. 151, Colbert, Edwin Harris, and Dirk Albert Hooijer, Bulletin of the American Museum of Natural History, vol. 102, art. 1 (1953); and No. 152, Haas, Georg, American Museum Novitates, no. 1729 (1955).

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Specimens of the two Mongolian ochotonids described here were collected by the Central Asiatic Expeditions of the American Museum of Natural History in 1928. Specimens of one, which seems to be near *"Ochotona" gobiensis*, offer new morphological evidence pertaining to the relationships of that species. The other ochotonid is a new genus and species.

I thank Dr. E. H. Colbert, Mrs. Rachel H. Nichols, and Dr. G. G. Simpson for allowing me to study, and for the loan of, these Mongolian specimens. I appreciate also the opportunity given by Dr. A. S. Romer to conduct part of the research reported here at the Museum of Comparative Zoölogy at Harvard College. Dr. L. E. Spock kindly assisted in a search for a Mongolian locality, and Dr. R. W. Wilson helpfully criticized the manuscript. The illustrations were prepared by Dr. Florence D. Wood. Finally, thanks are given for financial assistance from the Elizabeth Edwards Chace Fund of Smith College.

The abbreviation A.M.N.H. refers to specimens in the collections of the American Museum of Natural History. In the illustrations stippling on the teeth indicates the presence of cement.

A NEW GENUS FOR *"OCHOTONA" GOBIENSIS*

Figures 1, 2

A new species of ochotonid, *Ochotona gobiensis,* was described by Young in 1932,[1] based on specimens from the late Tertiary Tung Gur Basin near Irdin Manha in Inner Mongolia. Known material included a crushed skull, right upper jaw with P^3–M^1, two lower jaws with cheek teeth, and some fragmentary limb bones (Young, 1932, p. 255). Unfortunately these specimens, which were in the Chinese Laboratory of Cenozoic Research (now Institute of Vertebrate Paleontology and Paleoanthropology), seem to have been lost (Young, *in litt.,* October 21, 1959). The age of the specimens, which were found in beds below the Platybelodon beds, seems to be late Miocene ("Tung Gur Miocene," in Teilhard de Chardin and Leroy, 1942, p. 23). A specimen from the Pontian of Kansu that was figured in Boule *et al.* (1928, p. 96, fig. 23A) resembles Young's specimens (Bohlin, 1942b, p. 151) and may represent a later member of the same ochotonid line.

Four incomplete maxillae (A.M.N.H. Nos. 26244, 26246, 26247, and 26756), three partial lower jaws (A.M.N.H. Nos. 26757–26759), and an astragalus (A.M.N.H. No. 26760) of an ochotonid were collected by the

[1] Although Young's paper appeared in the Bulletin of the Geological Society of China for December, 1931, the manuscript was received for publication in March, 1932. Thus, 1932 is the date of publication for Young's species and is used here in reference to that paper.

Central Asiatic Expeditions "west of Sunnet Wong's near shallow lake, Mongolia." A complete upper cheek tooth series, P^2–M^2, is present (A.M.N.H. No. 26244); of the lower cheek teeth only P_3–M_1 are represented. The teeth that can be compared, P^3–M^1 and P_3–M_1, resemble in structure those of *Ochotona gobiensis* described and figured by Young (1932, pp. 255–256, figs. 1A–C), but the upper cheek teeth seem to be larger in the American Museum specimens (table 1). Whether the size differences represent variation within a species or between species can-

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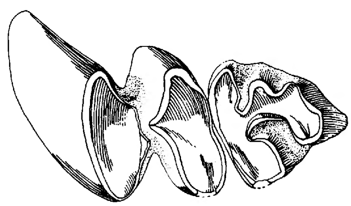

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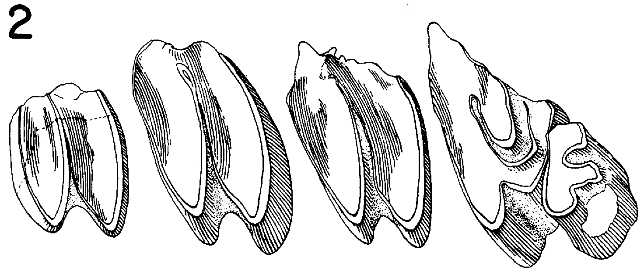


FIGS. 1, 2. *Alloptox* near *A. gobiensis*. 1. Occlusal view of left P_3–P_4, A.M.N.H. No. 26757. × 7. 2. Occlusal view of right P^2–M^2, A.M.N.H. No. 26244, buccal wall of M^2 restored from other specimens. × 6.5.

not be determined conclusively from the known specimens. No mention of "Sunnet Wong's, near shallow lake" was found in the field records for 1928 of the Central Asiatic Expeditions, and the exact stratigraphic level of this locality is unknown. Young (*in litt.*, October 21, 1959) is of the opinion that the specimens probably came from the same level as did his specimens of *O. gobiensis*. Thus the ochotonid represented by the American Museum specimens is similar in structure to *O. gobiensis* and may be of similar geologic age, but owing to an indication of size differences and uncertainties of stratigraphic position, these specimens are considered to be near and are not definitely assigned to Young's species. More definite assignment awaits more complete evidence.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Alloptox* (MEASUREMENTS OF *A. gobiensis* FROM YOUNG, 1932)

	A. gobiensis	A.M.N.H. No. 26244	*A.* near *A. gobiensis* A.M.N.H. No. 26246	*A.* near *A. gobiensis* A.M.N.H. No. 26247	A.M.N.H. No. 26756
P^2					
Anteroposterior	—	1.0	—	—	—
Transverse	—	1.8	—	—	—
P^3					
Anteroposterior	—	2.4	2.2	2.3	—
Width, anteroloph	—	2.3	2.1	2.4	—
Width, posteroloph	—	4.2	—	—	—
P^4					
Anteroposterior	—	2.3	2.3	2.4	2.3
Width, anteroloph	—	—	3.7	—	4.0
Width, posteroloph	—	4.2	3.9	4.2	4.0
M^1					
Anteroposterior	—	2.3	2.3	2.3	2.3
Width, anteroloph	3.0[a]	3.8	3.8	3.8	—
Width, posteroloph	—	3.7	3.8	3.6	3.7
M^2					
Anteroposterior	—	2.3	2.2	2.1	—
Width, anteroloph	—	—	3.3	3.0	—
Width, posteroloph	—	—	2.9	2.7	—
Length, P^3–M^2	—	10.9	10.2	10.1	—
Length, P^3–M^1	5.4[b]	8.6	7.7	*ca.* 7.8	—

[a] Breadth, M^1.

[b] Given as length of P^3–M^2 (Young, 1932, p. 256); as Bohlin noted (1942b, p. 151), this is incorrect and probably refers to length of P^3–M^1.

Kretzoi (1941, p. 111, fig. 2A) figured right P_3 of *Ochotona gobiensis* and stated in the caption for the figure, "*Metochotona* n.g. *gobiensis* (Young). Tung Gur-Obermiozän." No statement of characters was given for the new genus, and the name, which thus does not meet the requirements for availability of the International Rules of Zoological Nomenclature, is a *nomen nudum*. Whether or not Kretzoi considered the structure of P_3 to characterize his genus, the structure of that tooth in Young's specimens (Young, 1932, p. 256) and in A.M.N.H. Nos. 26757–26759 does suggest that a line generically distinct from *Ochotona* may be represented. In Young's specimens of *O. gobiensis* and in the American Museum specimens (fig. 1), P_3 has a shallower antero-external fold and a longer, more posteriorly extending, antero-internal fold than in Pliocene and later species of *Ochotona*.

TABLE 2
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Alloptox*
(MEASUREMENTS OF *A. gobiensis* FROM YOUNG, 1932)

	A. gobiensis	A.M.N.H. No. 26757	*A.* near *A. gobiensis* A.M.N.H. No. 26758	A.M.N.H. No. 26759
P_3				
Anteroposterior	—	2.1	2.3	2.0
Width, trigonid	—	1.5	1.7	1.6
Width, talonid	—	2.2	2.2	2.1
P_4				
Anteroposterior	—	2.4	2.6	2.3
Width, trigonid	—	2.4	2.4	—
Width, talonid	—	2.5	2.6	2.5
M_1				
Anteroposterior	—	—	—	2.4
Width, trigonid	—	—	—	2.4
Width, talonid	—	—	—	2.4
Length, P_3–M_3	10.5	—	—	—
Length, P_3–P_4	4.5	4.4	5.2	4.6
Length, M_1–M_3	6.0	—	—	—

Specimens of upper cheek teeth (fig. 2) offer further evidence that a line distinct from *Ochotona* may be represented. On the anterior wall of P^2, known from A.M.N.H. No. 26244, two distinct reëntrant folds occur, of which the outer is deeper and the inner is somewhat more widely open. Both folds persist along the shaft of the tooth. In *Ochotona* a single anterior reëntrant fold usually occurs on P^2; a small lingual fold is sometimes present but shallower than the inner anterior fold in A.M.N.H. No. 26244. Three specimens of M^2 are known from the American Museum specimens. That tooth has a long internal hypostria similar to that in *Ochotona,* but lacks the posteriorly directed process from the posteroloph that is characteristic of *Ochotona lagreli* and later species of *Ochotona.* Although P^2 and M^2 are not known in Young's specimens, resemblance to the American Museum specimens in the structure of those teeth might be expected on the basis of similiarity in other teeth.

The evidence seems to point, therefore, to the existence of a line of ochotonid that differed in several characteristics from the genus *Ochotona.* This line is here considered to be generically distinct from other known ochotonids. The diagnostic features given below are based on structures found both in Young's specimens and in the American Museum specimens; it seems probable that the characteristics of P^2 and

M^2 known from the American Museum specimens will prove also to be diagnostic for the new genus.

ALLOPTOX, NEW GENUS

DIAGNOSIS: Dental formula, $\frac{(2)}{1}, \frac{0}{0}, \frac{3}{2}, \frac{2}{3}$. Cheek teeth hypsodont. On P^3 crescentic fold connecting to anterobuccal wall; long internal hypostria on P^4, M^1, and M^2. On P_3 antero-external fold shallower than in *Ochotona;* long antero-internal fold extending postero-externally and reaching farther posteriorly than in *Ochotona;* enamel on posterior and buccal walls of antero-internal fold thicker than on anterior wall. Trigonid and talonid of P_4, M_1, and M_2 each about equal in width. Single column forming M_3. Probably the following can be added to the above: two persistent, well-developed anterior folds on P^2; posterior process from posteroloph of M^2 absent.

TYPE SPECIES: *Ochotona gobiensis* Young, 1932.

DISTRIBUTION: Late Miocene of Inner Mongolia; probably Pontian of Kansu.

In some characteristics, such as the absence of a posterior process on M^2 and the shallower antero-external fold on P_3, *Alloptox gobiensis* and *Alloptox* near *A. gobiensis* are more primitive than Pontian and later species of *Ochotona.* The well-developed antero-internal fold on P_3 in *Alloptox,* however, seems to be advanced beyond that fold in *Ochotona* and would not be expected in an ancestral line leading to *Ochotona.* Two anterior folds on P^2 are found in primitive lagomorphs such as *Mytonolagus* and *Desmatolagus vetustus* and also characterize several later ochotonids, including *Lagopsis* and *Prolagus.* In *Ochotona,* however, a single anterior fold is usually persistent on P^2, and a tendency towards such a condition of P^2, rather than the presence of two persistent folds, might be expected in the line leading to *Ochotona.* Thus, *Alloptox* seems not only distinct from *Ochotona* but also off the line leading to *Ochotona.* A second ochotonid, discussed below, may be closer to *Ochotona.*

A NEW GENUS AND SPECIES OF OCHOTONID

Specimens of a new ochotonid are from the Tairum Nor Basin of Inner Mongolia. The beds from which the fossils came have been described as part of the Tung Gur formation (Spock, 1929, p. 6), considered to be late Miocene in age (Colbert, 1939, pp. 6–7). Recent exploratory work has suggested that the beds at Tairum Nor are "Mio-Pliocene" in age and somewhat younger than the "late Miocene or slightly earlier" beds at Tung Gur (Chow and Rozhdestvensky, 1960, p. 5). According to the field notes for 1928 of Walter Granger, the specimens

TABLE 3
MEASUREMENTS (IN MILLIMETERS) OF UPPER CHEEK TEETH OF *Bellatona forsythmajori*

	A.M.N.H. No. 26242	A.M.N.H. No. 26761	A.M.N.H. No. 26763
P^2			
Anteroposterior	*ca.* 0.8	—	*ca.* 0.9
Width	*ca.* 1.7	—	*ca.* 1.6
P^3			
Anteroposterior	1.7	1.6	1.8
Width, anteroloph	1.8	1.7	2.1
Width, posteroloph	—	3.7	—
P^4			
Anteroposterior	1.8	1.7	1.8
Width, anteroloph	3.0	*ca.* 3.4	—
Width, posteroloph	—	—	3.2
M^1			
Anteroposterior	1.8	1.7	1.8
Width, anteroloph	—	3.2	3.3
Width, posteroloph	3.4	3.3	—
M^2			
Anteroposterior	1.8	1.7	—
Width, anteroloph	3.2	3.1	—
Width, posteroloph	—	—	—
Length, P^3–M^2	8.4	7.9	—

came from red beds below sandstone. Exact levels of different specimens within the red beds are not given in the notes.

Known upper cheek teeth are relatively homogeneous in size (table 3), but lower cheek teeth are more variable (tables 4 and 5). Most lower cheek teeth vary over a fairly continuous size range, but one specimen having M_1–M_3 (A.M.N.H. No. 26767) is separated from the others by a gap in size. This specimen, which is near the size of *Alloptox* near *gobiensis* and possibly referable there, is excluded from consideration with the other specimens and from the statistical treatment. Coefficients of variation for the lower cheek teeth are higher than average for a homogeneous sample (Simpson *et al.*, 1960, p. 91, suggest a range of V between 4 and 10 for linear dimensions of mammalian anatomical elements, and average values of 5 or 6). There is variation also in the pattern of the occlusal surface of M^2 and of P_3.

Variation in size and in tooth pattern of the sort exhibited by these specimens raises the question of whether the specimens represent a single species. The variation is fairly continuous with regard to both size

TABLE 4

MEASUREMENTS (IN MILLIMETERS) OF LOWER CHEEK TEETH AND JAWS OF *Bellatona forsythmajori*

	A.M.N.H. No. 26770	A.M.N.H. No. 26237	A.M.N.H. No. 26768
P_3			
Anteroposterior	1.5	1.4	1.1
Width, talonid	1.8	—	1.3
P_4			
Anteroposterior	1.9	1.7	1.7
Width, trigonid	1.8	1.8	1.5
Width, talonid	1.9	1.8	1.6
M_1			
Anteroposterior	1.8	1.7	1.8
Width, trigonid	1.9	1.9	1.6
Width, talonid	1.9	—	1.7
M_2			
Anteroposterior	—	1.8	1.8
Width, trigonid	—	1.9	1.7
Width, talonid	—	1.8	1.6
M_3			
Anteroposterior	—	—	0.4
Width	—	—	1.2
Length, P_4–M_2	—	5.9	5.3
Inside depth of jaw, M_1	9.3	8.9	7.9

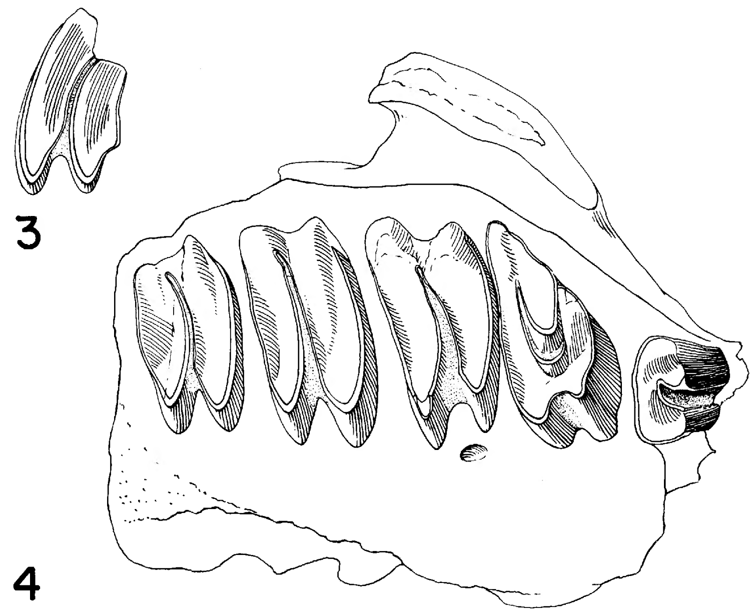
and pattern, however, and no breaks that would allow distinction between different taxa can be discerned. Further, there is evidence from the lower cheek teeth that another factor, differences in ontogenetic age, may account for much of the variation. In the smallest lower jaw, P_3 and P_4 exhibit relatively little wear, indicating youth of the individual represented. Small specimens tend to have a less distinct antero-external groove on P_3 than do larger specimens. This difference could be due to age; deepening of folds on P_3 with age is known to occur in some other lagomorphs (e.g., Dawson, 1958, p. 40). In view of the fairly continuous variation and the evidence that age differences account for much of the variation, the specimens are here interpreted as members of a single species.

Bellatona forsythmajori, new genus and new species

Figures 3–7

DIAGNOSIS: Dental formula, $\frac{(2)}{1}, \frac{0}{0}, \frac{3}{2}, \frac{2}{3}$. Cheek teeth hypsodont. Single anterior fold on P^2; P^3 having crescentic fold that retains buccal con-

nection, and short internal hypostria; long internal hypostria on P^4, M^1, and M^2; M^2 variable, having on posterior wall a rounded posterior process or only a slight protrusion. Lower incisor extending posteriorly to below talonid of M_1 or trigonid of M_2. On P_3 antero-external groove varying from shallow to distinct in specimens that are probably adult; trigonid and talonid of P_4, M_1, and M_2 about equal in width; single col-



FIGS. 3, 4. *Bellatona forsythmajori.* 3. Occlusal view of left M^2, A.M.N.H. No. 26242. 4. Occlusal view of right P^2–M^2, with incomplete maxilla and palatine, A.M.N.H. No. 26761, with P^2 restored from A.M.N.H. No. 26241. $\times$ 7.5.

umn forming M_3. Posterior mental foramen below talonid of M_1 or trigonid of M_2.

TYPE SPECIMEN: A.M.N.H. No. 26770, incomplete right lower jaw having P_3–M_1.

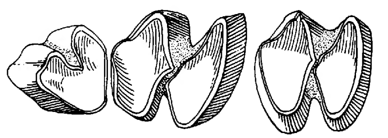
REFERRED SPECIMENS: A.M.N.H. Nos. 26241, 26242, 26761, 26763, fragmentary right and left maxillae with cheek teeth and associated parts of palatines; A.M.N.H. Nos. 26235–26240, 26605, 26762, 26764–26766, 26768, 26769, 26771, incomplete right and left lower jaws with dentition.

HORIZON AND LOCALITY: Upper Miocene or "Mio-Pliocene"; red beds below sandstone, Tairum Nor Basin, Inner Mongolia.

Description

Dentition: No specimens of upper and lower jaws are known to have been found in occlusal association. However, the known upper cheek teeth are of a size that could occlude with the "adult" lower teeth discussed below. No other ochotonid, with the exception of the larger specimen (A.M.N.H. No. 26767) is known from the locality, and association of upper and lower jaws is most probable.

The upper incisors are unknown. The most anterior upper cheek tooth, P^2, has a relatively straight shaft; a cement-filled reëntrant fold is present approximately in the midline of the anterior surface. The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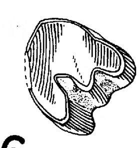
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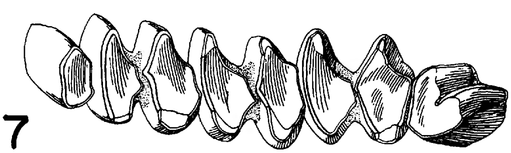
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Figs. 5–7. *Bellatona forsythmajori*. 5. Occlusal view of right P_3–M_1, type, A.M.N.H. No. 26770. × 7. 6. Occlusal view of right P_3, A.M.N.H. No. 26766. × 7.5. 7. Occlusal view of left P_3–M_3, A.M.N.H. No. 26768, probably a young individual. × 7.

shafts of P^3–M^2 curve outward in the maxillary tuberosity. On P^3 the anterior loph crosses about half of the width of the occlusal surface. That tooth has a cement-filled, crescentic fold, which is connected with the antero-external wall of the tooth, and a short, wide internal hypostria. A long, cement-filled, internal hypostria divides each of the more posterior cheek teeth, P^4, M^1, and M^2, into an anterior and a posterior loph; buccally the two lophs of each tooth are joined by a narrow bridge. The hypostria on P^4 is slightly shorter relative to the width of the tooth than are the hypostriae on the molars. Distinct transverse ridges are formed by the enamel on the anterior walls of both lophs of P^4–M^2.

The posterior wall of M^2 is variable. In A.M.N.H. No. 26242 (fig. 3) a rounded, posteriorly directed process, which persists up the shaft, is present. In A.M.N.H. No. 26241 M^2 is broken at the occlusal surface, but a piece of that tooth in the maxillary tuberosity has a protrusion

TABLE 5

Statistical Data on Lower Cheek Teeth of *Bellatona forsythmajori*

	N	*O.R.*	*M*	*s*	*V*
P_3					
Anteroposterior	9	1.1–1.5	1.32	0.13	9.8
Width, talonid	7	1.3–1.8	1.63	0.17	10.4
P_4					
Anteroposterior	12	1.5–2.0	1.75	0.14	8.0
Width, trigonid	10	1.5–2.0	1.79	0.14	7.8
Width, talonid	9	1.6–2.0	1.80	0.12	6.7
M_1					
Anteroposterior	12	1.6–2.0	1.78	0.13	7.3
Width, trigonid	12	1.5–2.1	1.85	0.18	9.7
Width, talonid	10	1.7–2.3	1.89	0.19	10.0
M_2					
Anteroposterior	9	1.5–2.0	1.74	0.15	8.6
Width, trigonid	10	1.6–2.1	1.82	0.18	9.9
Width, talonid	7	1.6–2.1	1.78	0.20	11.2

N, number of specimens.
O.R., observed range.
M, mean.
s, standard deviation.
V, coefficient of variation.

from the posteroloph that seems to represent the process. In A.M.N.H. No. 26761 (fig. 4), however, M^2 lacks a distinct posterior process, although on the occlusal surface there is a slight posterior protrusion, which can be detected also on the shaft. The variable development of the process seems to be a matter of individual differences, not of differences in ontogenetic age. The lack of uniformity of the process in *Bellatona* may indicate that the character was recently initiated in this line of ochotonid. Even where better developed, as in A.M.N.H. No. 26242, the process in *Bellatona* is less clearly set off from the posteroloph than in *Ochotona,* in which the process is characteristically present and distinct.

The lower incisor resembles in shape that in Recent *Ochotona.* The shaft of the incisor, as indicated by a swelling on the medial surface of the jaw, extends to a line below the talonid of M_1 or the trigonid of M_2. The incisor in Recent *Ochotona* is shorter, extending usually to below the talonid of P_4 or the trigonid of M_1.

The occlusal pattern of P_3, the most anterior lower cheek tooth, in

specimens that are probably fully grown, seems to be that present in A.M.N.H. Nos. 26770 (fig. 5), 26762, and 26237; the size of these specimens is such that occlusion with the known upper cheek teeth would be possible. On P_3 a postero-external, cement-filled fold, which is between trigonid and talonid, crosses somewhat less than half of the width of the occlusal surface. On the trigonid these specimens have a wide, shallow, antero-external groove, and in A.M.N.H. Nos. 26770 and 26762 the antero-internal wall of the trigonid is slightly concave. In A.M.N.H. No. 26766 (fig. 6) an individual variant on the adult pattern seems to be present. In this specimen the antero-external groove is deeper than in the above specimens and is filled with cement, and a more distinct antero-internal concavity is present.

Other specimens having P_3 seem to represent younger individuals. In the smallest specimen having P_3, A.M.N.H. No. 26768 (fig. 7), the premolars seem to be in a relatively early stage of wear. P_3 is flattened antero-externally on the trigonid. This flattening seems to characterize younger individuals and is found also on P_3 in A.M.N.H. No. 26764. Specimens such as A.M.N.H. Nos. 26236, 26769, and 26771 are a little below adult size and have a shallower antero-external groove on the trigonid than do A.M.N.H. Nos. 26770, 26762, and 26237.

The more posterior cheek teeth exhibit less variation in shape than does P_3. On P_4–M_2 the trigonid is approximately equal in width to the corresponding talonid but is longer anteroposteriorly. The trigonids of M_1 and M_2 have an anteriorly directed protrusion. The posterior wall of each trigonid forms a wide V, whereas that of each talonid is straighter. Enamel on the posterior wall of the trigonids and the talonids forms distinct transverse ridges. The single column that composes M_3 is tapered buccally and rounded lingually. In general, P_4–M_3 resemble those teeth in Recent *Ochotona,* although the anterior protrusion of the trigonids of M_1 and M_2 seems to be less in the fossil.

SKULL AND JAW FRAGMENTS: Of the skull, only parts of the maxillary and palatine bones and the anterior part of the zygoma are present. The concavity for the masseter muscle on the outer surface of the zygoma does not extend so far anteriorly as in Recent *Ochotona* and resembles more closely that in *O. lagreli* (Bohlin, 1942a, p. 44, fig. 11B). As in *O. lagreli* (Bohlin, 1942b, pp. 149–150, fig. 21B), the contact of the zygoma with the maxillary tuberosity extends farther posteriorly than in Recent *Ochotona.* On the palate, the premolar foramen occurs in line with P^4.

In shape the horizontal ramus of the lower jaw is similar in general to that in Recent *Ochotona.* On the lateral surface of the jaw several foramina, of which one may be larger than the others, occur in line with

the premolars. Near the ventral edge of the jaw a more posterior mental foramen occurs approximately in line with the talonid of M_1 or the trigonid of M_2. In Recent *Ochotona* the corresponding mental foramen is more posterior in position, usually occurring below the middle or the talonid of M_2.

Discussion

Comparisons of *Bellatona* with *Ochotona* indicate that the two genera differ mainly in characteristics in which the former seems to be more primitive. The general pattern of the upper cheek teeth is similar, but *Bellatona* is primitive in having a less distinct posterior process on M^2. Of the lower cheek teeth, P_3 in *Bellatona* lacks the well-developed folds that are found on the trigonid in *Ochotona*. However, *Bellatona* shows a shallow antero-external groove and, in some specimens, a suggestion of an antero-internal concavity on the trigonid of P_3. A deepening of the groove and the development of an antero-internal fold in place of the concavity would result in the pattern of P_3 found in *Ochotona*. The more posterior cheek teeth, P_4–M_3, are similar in general to those in *Ochotona*.

Structurally, then, *Bellatona* could be on or very near the line leading to *Ochotona*. *Bellatona* seems to be late Miocene, or possibly "Mio-Pliocene," in age. The earliest recorded appearance of *Ochotona* seems to be Pontian in Asia (Teilhard de Chardin and Leroy, 1942, p. 23, list *Ochotona lagreli* from the Pontian of Kansu and Shansi and the middle Pliocene of Ertemte) and is probably Pontian in eastern Europe also (Khomenko, 1914, p. 15, names *Proochotona* from the Maeotic; *Proochotona* resembles *Ochotona* closely and has been referred to *Ochotona* by Argyropulo and Pidoplichka, 1939, p. 723). Although there is some question about the exact age of some Asian "Pontian" faunas (e.g., Shotwell, 1956, p. 719; Simpson, 1947, pp. 623, 666), most of those faunas seem to be early Pliocene or later in age. Thus, temporally as well as structurally *Bellatona* could represent a line leading towards *Ochotona*.

The earlier relatives of *Bellatona* are difficult to trace, owing in part to the absence of a known fossil record of ochotonids in the earlier Miocene of Asia. Of known late Oligocene forms in Asia, *Sinolagomys* would seem on the basis of several progressive dental characteristics to be closer to the line leading to *Bellatona* than is the relatively primitive *Desmatolagus gobiensis*. Bohlin (1942a, pp. 83–85, 107), however, considers *Sinolagomys* to be off the line leading to *Ochotona* for reasons that would exclude *Sinolagomys* from the ancestry of *Bellatona* also. Perhaps the known fossil record does not include the line ancestral to *Bellatona*. At

any rate, *Bellatona* seems to be closer to the known late Oligocene ochotonids of Asia than to the late Oligocene and Miocene ochotonids, *Amphilagus, Titanomys, Lagopsis,* and the *Piezodus-Prolagus* line, that were present in western Europe.

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